THE PELYCOSAURIAN (AMNIOTA: SYNAPSIDA) ASSEMBLAGE FROM THE LATE PENNSYLVANIAN SANGRE DE CRISTO FORMATION OF CENTRAL COLORADO

STUART S. SUMIDA[1]

DAVID S BERMAN
Curator, Section of Vertebrate Paleontology

ABSTRACT

A diverse assemblage of pelycosaurian-grade synapsids is described on the basis of fragmentary remains from a highly fossiliferous quarry of Late Pennsylvanian, probably Missourian, age in the Sangre de Cristo Formation of central Colorado. The fragmentary nature of the materials precludes in most instances assignment below family or subfamily, or the erection of new taxa. Identifications include at least one member each of the families Ophiacodontidae, Sphenacodontidae, and Hapto-dontidae, and two members of the Edaphosauridae, one referable to *Ianthasaurus* and the other to a new but unnamed genus and species. Only the extremely productive Garnett quarry of eastern Kansas and El Cobre Canyon in northern New Mexico have yielded as many Pennsylvanian-aged pelycosaurian taxa with certainty.

INTRODUCTION

Localities of Pennsylvanian age that yield remains of terrestrial tetrapods are extremely rare, and those that produce pelycosaurian-grade synapsids are even fewer in number. Of the well-known North American localities (Table 1), Vaughn (1969, 1972) described one in central Colorado that includes as many or more species of pelycosaurs than any other in the world. The quarry, designated as the "Badger Creek locality" by Milner and Panchen (1973) in their review of Late Paleozoic tetrapod faunas and localities, is in the Sangre de Cristo Formation near the town of Howard in the Arkansas River valley of Fremont County, Colorado. Vaughn (1972:2) described the productive level of the quarry as a two- to three-foot-thick black shale that is a "lens-shaped deposit that probably represents a pond, perhaps an oxbow within the general system of stream channels indicated in this part of the formation." The black shale unit was designated by Brill (1952) as part of "Interval 300," lying approximately 442 m above the base of the 2933 m-thick Sangre de Cristo Formation. It lies in NW ¼ NE ¼ SW ¼ Sec. 22, T. 49 N, R. 10 E. Vaughn estimated that the deposit is of Late Pennsylvanian age, most likely Missourian, primarily on the basis of the vertebrate assemblage; however, he also considered geological evidence based on the work of Mallory (1958, 1960).

Although specimens from the Badger Creek locality are rarely complete, they show little or no sign of surface wear. This has facilitated identification of a highly diverse assemblage that, in addition to pelycosaurs, includes elasmobranch and palaeoniscoid fishes, labyrinthodont, aistopod, and microsaurian amphibians, the enigmatic diadectomorphs *Desmatodon* and *Limnoscelis,* and protorothyridid reptiles (Vaughn, 1969, 1972; Berman and Sumida, 1990).

Table 1.—*Numbers of pelycosaurian taxa from Pennsylvanian localities in North America. Localities are listed in approximate order from east to west. * Pittsburgh is actually two (or more) deposits.*

Locality	Number of pelycosaur taxa	Reference
Florence, Nova Scotia	5	Reisz, 1972
Joggins, Nova Scotia	1(?)	Carroll, 1964
Pittsburgh, Pennsylvania*	2	Romer, 1952, 1961
Elm Grove, West Virginia	1	Berman, 1979
Linton, Ohio	1	Hook and Baird, 1986
Danville, Illinois	1	Cope, 1875
Jasper County, Illinois	1	De Mar, 1970
Robinson, Kansas	1	Chorn and Schultze, 1990
Garnett, Kansas	5	Reisz, 1990
Hamilton, Kansas	1	Schultze and Chorn, 1988
Badger Creek, Colorado	5	This paper
El Cobre Canyon, New Mexico	7	Berman, in press

Vaughn (1972) recognized the presence of four pelycosaurian taxa among the Badger Creek materials. Additional preparation, however, has revealed at least five different pelycosaurs. Only the localities of Garnett, Kansas, and possibly Florence, Nova Scotia, have yielded as many different kinds of Pennsylvanian pelycosaurs. The Badger Creek remains include at least one member each of the family Ophiacodontidae and the subfamilies Sphenacodontinae and Haptodontinae, and two members of the Edaphosauridae, one referable to *Ianthasaurus* and the other to a new but unnamed genus and species.

All of the specimens described in this study were collected by Peter Vaughn and cataloged into the University of California, Los Angeles, vertebrate paleontology collections (UCLA VP). In 1987, this collection, as well as others from the Permo-Pennsylvanian at that institution, were transferred permanently to the Carnegie Museum of Natural History, Pittsburgh (CM).

SYSTEMATIC DESCRIPTIONS

Recent analyses of the phylogenetic relationships of primitive amniotes (Gauthier et al., 1988; Berman et al., 1992) have proposed the Synapsida as amniotes separate from a more narrowly defined Reptilia. No subsequent proposal of nomenclature regarding the class designation of pelycosaurs, traditionally referred to as "mammal-like reptiles," has been forthcoming. For that reason, class designations have been omitted in the following systematic descriptions.

Subclass Synapsida
Order Pelycosauria
Family Ophiacodontidae

Materials.—CM 31389, greater part of left humerus (Fig. 1A, B); CM 47693 (formerly UCLA VP 1695), partial neural arch; CM 47694 and 47695 (formerly UCLA VP 1696 and 1697), partial right and left ilia, respectively; CM 47696, part and counterpart blocks that include associated elements of most of left hindlimb and foot, right femur, and gastralia; CM 47705, nearly complete right pelvic girdle (Fig. 1C).

Description.—Though no cranial materials attributable to Ophiacodontidae are preserved, several postcranial elements exhibit features characteristic of the fam-
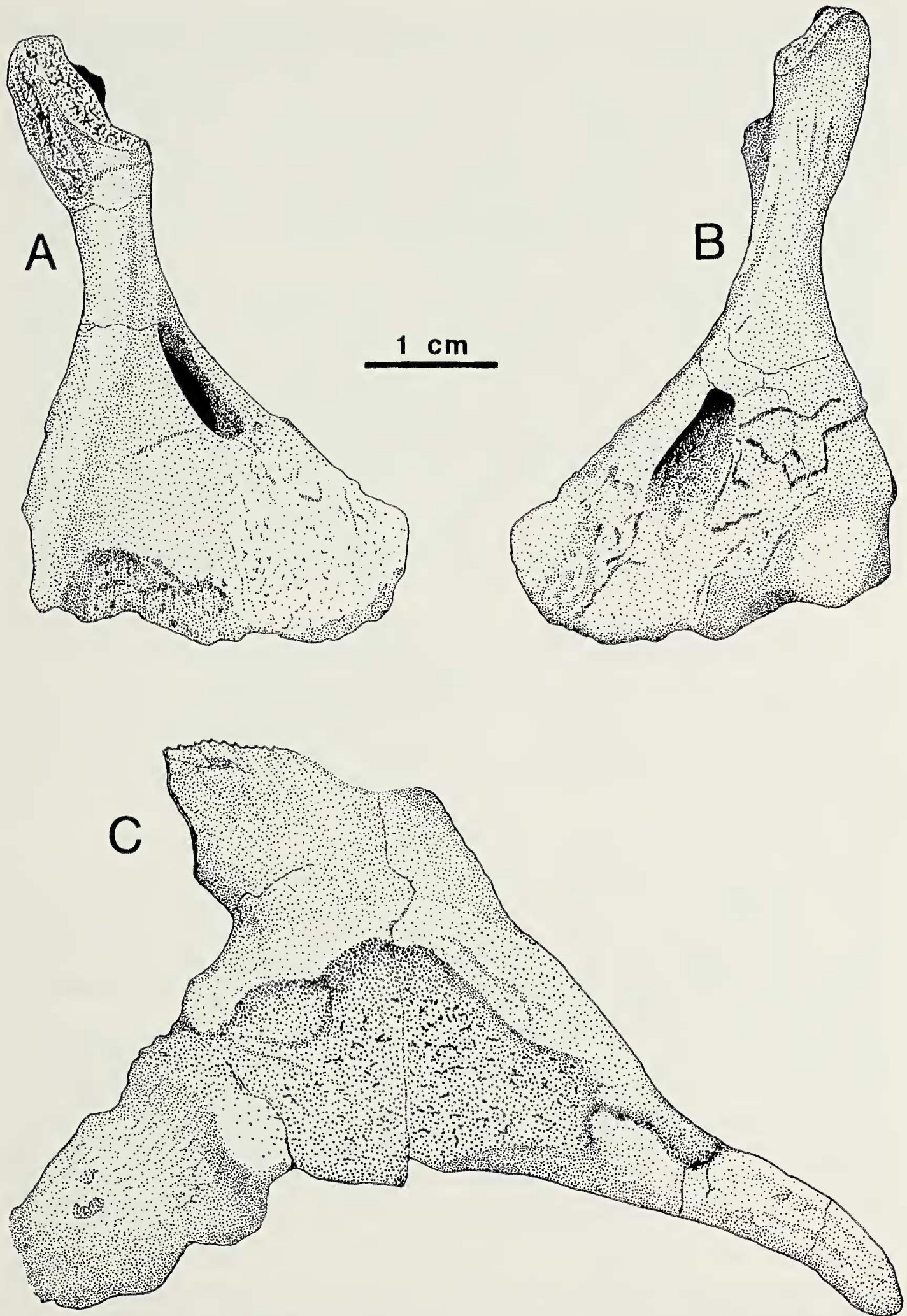
Fig. 1.—Ophiacodontid. A, B, distal dorsal and distal ventral views of left humerus CM 31389; C, lateral view of right pelvis CM 47705.

ily. Vaughn (1969) identified a partial neural arch, retaining only the left posterior zygaphophysis and base of the spine (CM 47693), and partial right and left ilia (CM 47694 and 47695 respectively) as ophiacodontid and appropriate to one another in size. Vaughn (1969) considered the neural arch as undoubtedly ophiacodontid, noting the laterally compressed blade-like structure of the spine and the absence of any lateral excavation of the neural arch. His assignment of the ilia was less certain, noting only their close similarity to those of Lower Permian *Ophiacodon* species figured by Romer and Price (1940) and the absence of features of other well-known groups. The ilia are of the same size and could very likely belong to the same individual.

Several other postcranial elements now recognizable from the Badger Creek locality help to confirm the presence of an ophiacodontid. This is particularly true of a nearly complete right pelvis (CM 47705, Fig. 1C). It is much smaller than that represented by the ilia CM 47694 and 47695, yet its sutures are not distinct. Although the distal tip of the iliac blade is missing, there is no doubt that the ilium tapered as it curved strongly posteriorly in typical ophiacodontid fashion. As in other pelycosaurs, within the rather simple, horizontally oval acetabular depression is a roughly triangular unfinished articular surface. A thin, poorly developed ridge defines the apex of the articular surface, which has the outline of a low, rounded, posteriorly directed wave crest. The ischium is a smoothly finished quadrangular plate, whereas the pubis is extremely slender and lightly built.

A humerus (CM 31389, Fig. 1A, B; see also Sumida, 1989a, fig. 15D) exhibits an extremely well-developed and elongate entepicondyle that is characteristic of the family. The distal terminus of the entepicondyle is rugose on both dorsal and ventral surfaces, presumably for the attachment of extensor and flexor musculature of the antebrachium, respectively. The ectepicondyle and tip of the supinator process are chipped away, but a groove that begins well up the slender shaft clearly separated them as in *Ophiacodon* (Reisz, 1986). Most of the proximal articular surface has been lost.

Part and counterpart blocks (CM 47696, Fig. 2) preserve most of an ophiacodontid left hindlimb and foot, greater part of the right femur, and numerous scattered gastralia. As is common in ophiacodonts, the articular surfaces of the limb bones are largely unossified. Both femora are visible in dorsal aspect only, and little description may be added beyond what is visible in Fig. 2. The tibia is approximately 65% of the length of the femur. The shaft of the tibia appears to be dorsoventrally compressed.

Elements of the hind foot are scattered and incomplete but sufficient to make some general comments. What appears to be the calcaneum is subcircular in outline, with the margins being thickened slightly over the central area. A notch for a perforating artery is not obvious in the specimen. What may be the neck of the astragalus is preserved adjacent to the calcaneum. The metatarsal elements are much longer than the phalanges. Although the jumbled nature of phalangeal elements prevents a detailed description, the presence of a claw-like distal phalanx

→

Fig. 2.—Ophiacodontid CM 47696, part and counterpart blocks showing associated elements of most of left hindlimb and foot, right femur, and scattered gastralia. Abbreviations: c, calcaneum; f, femur; fib, fibula; f imp, impression of femur; gast, gastralia; mett, metatarsal elements; p dist, distal phalanx; t, tibia; t imp, impression of tibia.
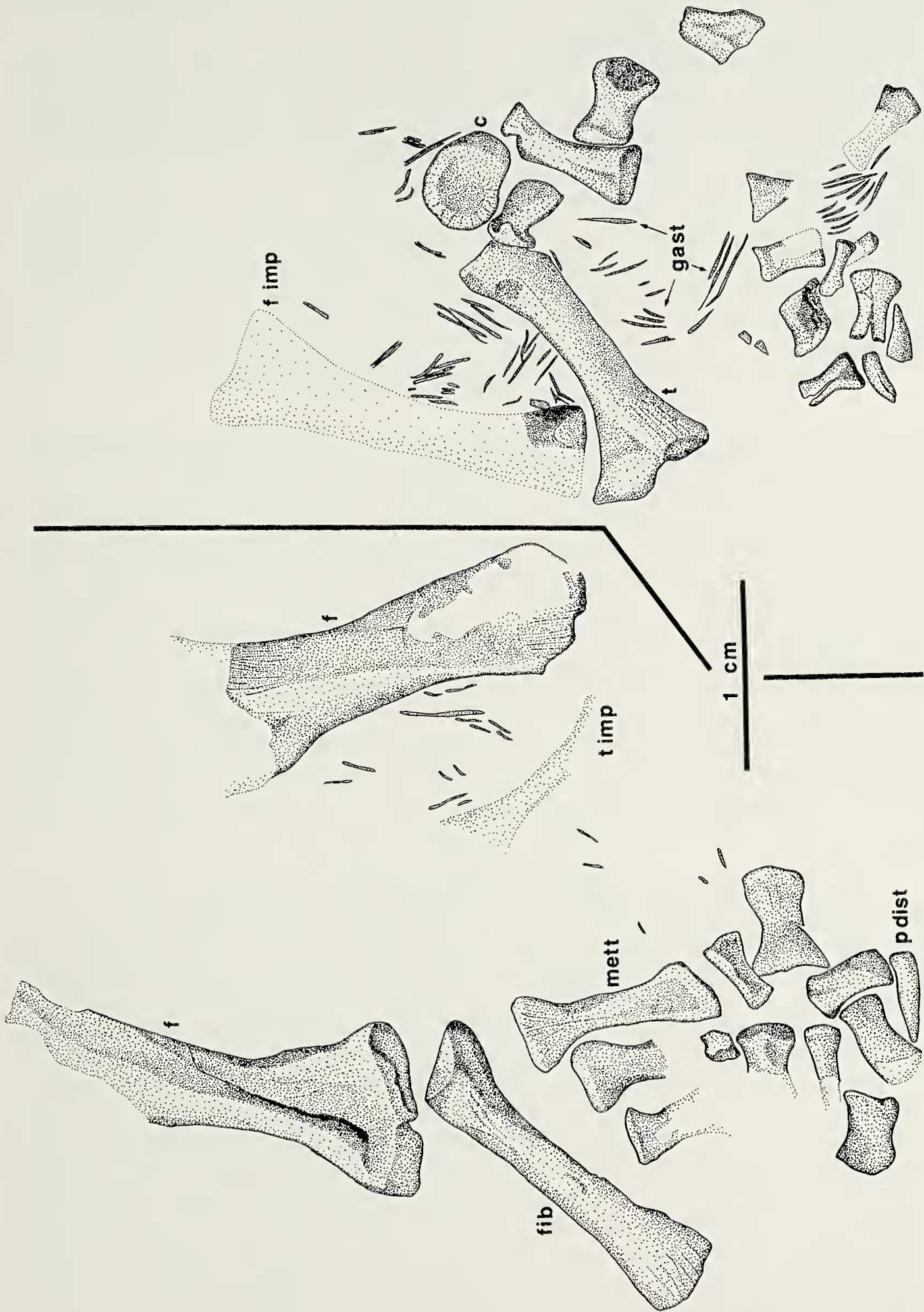
is notable. The phalanges are not broad and flattened as in some ophiacodonts such as *Ophiacodon* sp. (Romer and Price, 1940), indicating that the Badger Creek form may represent a primitive member of the family.

Gastralia are scattered among the hindlimb elements of CM 47696. None demonstrate the V-shaped bar appearance of the midline gastralia described in *Ophiacodon* (Romer, 1956). They are all thin, simple, rod-shaped elements similar to the more distal, lateral components of the ventral dermal armor described by Williston and Case (1913) in *Ophiacodon*.

Vaughn (1972) noted briefly the occurrence of an isolated basiparasphenoid (CM 47653, formerly UCLA VP 1740) among the Badger Creek materials that he believed to be ophiacodontid. This element actually belongs to a partial, disarticulated skeleton that was designated as the holotype of a new species of *Limnoscelis*, *L. dynatis* (Berman and Sumida, 1990).

<div align="center">

Family Sphenacodontidae
Subfamily Sphenacodontinae

</div>

Materials.—CM 34447, sacral vertebra (Fig. 3D); CM 34448, marginal tooth; CM 47702 (formerly UCLA VP 1704), partial left premaxilla (Fig. 3A); CM 47704 (formerly UCLA VP 1741), dorsal vertebra (Fig. 3B, C).

Description.—What Vaughn (1969) described as a fragmentary right maxilla of a sphenacodontine is reinterpreted here as a partial left premaxilla (CM 47702, Fig. 3A). The reinterpretation is based mainly on the presence of a large, well-preserved maxillary process that was laterally overlapped by the maxilla, and a large, flat symphyseal surface that contacted its mate on the midline. In general, the premaxilla compares closely to that in *Sphenacodon* (Eberth, 1985); however, it appears to possess only two robust teeth rather than three, and the second tooth (7 mm long) is considerably shorter than the first (11 mm long). As described by Vaughn (1969), the teeth are flattened slightly mediolaterally, broadly based, and distally pointed. The maxillary process angles posterodorsally, as is characteristic of sphenacodontines. The body of the premaxilla is robustly constructed, more so than those assigned to *Haptodus* (see below), as has been discussed by Reisz et al. (1992).

A nearly 15 mm-long isolated tooth (CM 34448), of somewhat different character, is nonetheless clearly sphenacodontid in nature. It is recurved and mediolaterally compressed. Distinct, low, very narrow cutting edges extend nearly the entire fore and aft lengths of the tooth, passing through the tip of the crown. The cutting edges are accentuated by a very shallow, parallel depression on what is probably the lingual surface of the tooth. This general morphology is in contrast to the somewhat more bulbous teeth assigned here to *Haptodus* (see below).

Vaughn (1972) noted the presence of a small sphenacodontid dorsal vertebra, CM 47704 (Fig. 3B, C), consisting of a centrum and neural arch with only the base of the neural spine preserved. A sphenacodontid sacral vertebra, CM 34447, of similar size and proportion is also present among the Badger Creek materials (Fig. 3D). As preserved, the vertebrae do not exhibit any features that would positively identify them as belonging to either a sphenacodontine or haptodontine. Assignment to the Sphenacodontidae rather than the Haptodontidae is based on the relatively much deeper lateral excavations in the neural arch just above the transverse processes and the very deep longitudinal excavations of the lateral surfaces of the centrum that result in the greatly flared rims. Reisz and Berman (1986) described similar but much shallower excavations in the primitive eda-
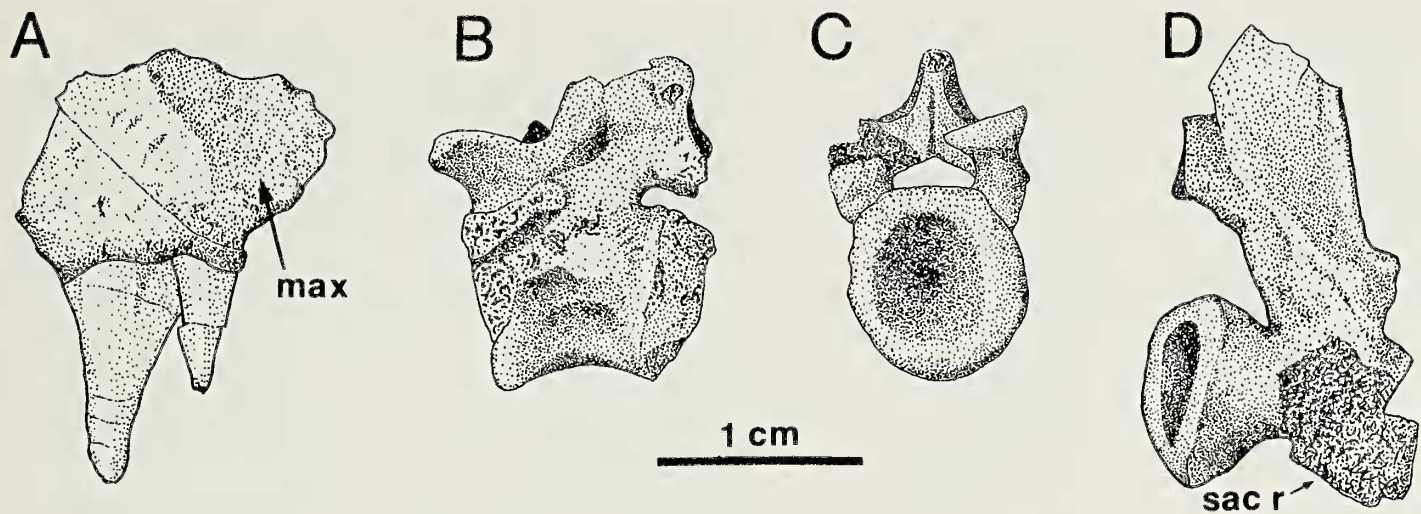
Fig. 3.—Sphenacodontid. A, lateral view of partial left premaxilla CM 47702; B, C, left lateral and anterior views of incomplete dorsal vertebra CM 47704; D, right posterolateral view of partial sacral vertebra CM 34447. Abbreviations: max, maxillary suture; sac r, articulation for sacral rib.

phosaur *Ianthasaurus*. Further, the configurations of the neural arch and associated spine are unlike those of the edaphosaurs found at Badger Creek. Brinkman and Eberth (1983) have pointed out that the varanopseid *Varanops* also possesses depressions of the neural arch, but their position is relatively more posterior. The midventral region of the centrum of CM 47704 is not sharply keeled, and the transverse processes, though broken, appear to be very small, indicating a position in the posterior region of the presacral column. Though only the base of the neural spine is present, its outline in horizontal section at the break is suggestive of a blade-like structure. In the sacral vertebra CM 34447 (Fig. 3D) the rib has been broken away and the cross-sectional area of the break is indicative of the first or second sacral vertebra. It also possesses the characteristic excavation of the neural arch and retains a blade-like neural spine. The costal articulations are stoutly buttressed.

Family Haptodontidae
Subfamily Haptodontinae

Materials.—CM 34443, partial right pterygoid (Fig. 4D); CM 34444, portion of right scapula (Fig. 4H); CM 34445, partial right femur (Fig. 4I); CM 34446, partial right dentary (Fig. 4E–G); CM 47701 (formerly UCLA VP 1749), left premaxilla (Fig. 4A, B); CM 47703, left premaxilla (Fig. 4C).

Description.—A right dentary, CM 34446 (Fig. 4E–G), is the most distinctly haptodontid element preserved at Badger Creek. The pattern of surface sculpture is very similar to that of *Haptodus garnettensis* (Laurin, in press), consisting of a series of fine, shallow, irregularly placed, interconnected pits and grooves. The teeth are sphenacodontid in nature, but show little of the differentiation characteristic of *Sphenacodon, Dimetrodon,* and other advanced sphenacodontids. In contrast to most sphenacodontids, the depth of the preserved anterior portion of the dentary remains uniform and is relatively much deeper throughout its length. In sphenacodontids there is a distinct narrowing of the dentary just before the symphyseal region, where it deepens in a strong dorsalward expansion. The expansion, with its greatly developed teeth, is accommodated by a corresponding dorsalward, step-like concavity of the ventral margin of the maxilla and the premaxilla, where there is a reduction or gap in the marginal dentition.
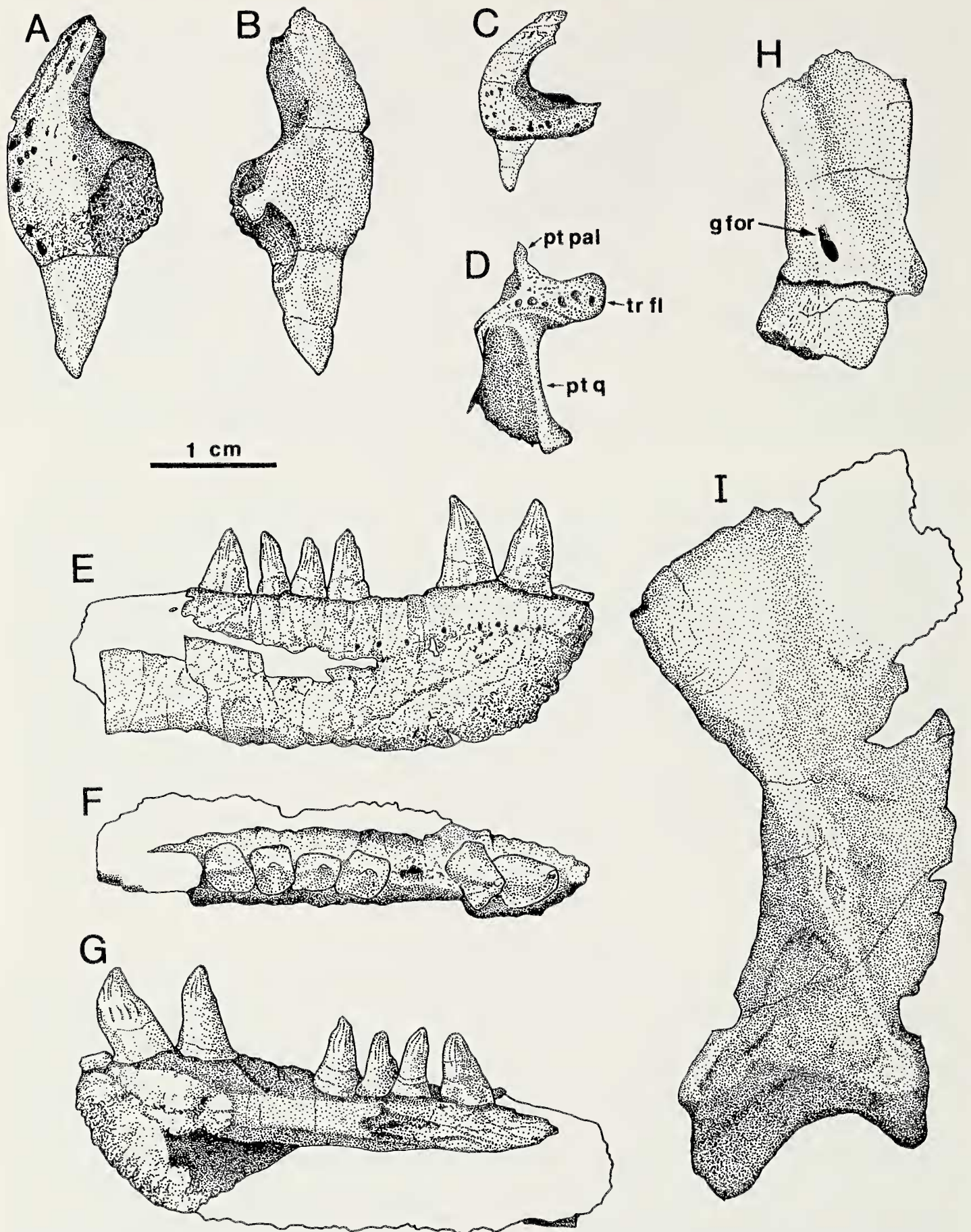
Fig. 4.—Haptodontine. A, B, lateral and medial views of larger left premaxilla CM 47701; C, lateral view of left premaxilla CM 47703; D, ventral view of partial right pterygoid CM 34443; E–G, lateral, dorsal, and medial views of partial right dentary CM 34446; H, lateral view of partial right scapular blade CM 34444; I, ventral view of right femur CM 34445. Abbreviations: g for, glenoid foramen; pt pal, palatal ramus of pterygoid; pt q, quadrate ramus of pterygoid; tr fl, transverse flange of pterygoid.

The symphyseal suture is rugose and approximately triangular in outline. The absence of a splenial reveals a moderately developed alveolar shelf along the dorsal margin of the medial surface of the dentary. Six teeth are preserved in the dentary, with a gap for another between the second and fourth. The teeth are somewhat bulbous and more stoutly conical than in other specimens of *Haptodus*. The third tooth appears to be permanently lost, inasmuch as the alveolus is completely filled with bone. Unlike sphenacodontids, but as occurs in some *Haptodus* specimens, the first two teeth are subequal in size and not greatly enlarged over those of the rest of the series. The posterior four teeth of the series are subequal in size. They are similar to those of *Haptodus* in being essentially simple, subconical structures. The bases, approximately the lower two-thirds of the teeth, are subcircular to quadrangular in horizontal section, whereas the crowns are circular with a slight posterolingual curvature. Shallow, minute grooves on the crown converge on the sharply pointed tip. In clear contrast to the marginal teeth of sphenacodontids, they are not compressed labiolingually and lack fore and aft cutting ridges. As with the premaxillary tooth, they are only slightly recurved. Although the two anteriormost teeth are larger than the rest, they do not show the extreme hypertrophy common to more advanced sphenacodontids.

The two left premaxillae, CM 47701 and 47703 (Fig. 4A–C), are of quite different sizes, but both are assigned to the Haptodontidae on the basis of the strong similarity of their surface sculpturing and tooth morphology to that of the partial dentary described above. Both premaxillae possess a large, anteriormost tooth, but sockets for two smaller, posterior teeth are present in the smaller, more complete specimen. The large, anteriormost tooth projects normal to the ventral plane of the body of the premaxilla, and its tip is only slightly recurved as in *Haptodus*. The distal portion of the dorsal process in the larger specimen is lost, but is clearly stouter than that of the smaller specimen.

A partial right pterygoid, CM 34443 (Fig. 4D), includes the transverse flange, quadrate ramus, and proximal portion of the palatine ramus. Although typically sphenacodontian in construction, it is too small to be associated with the robust sphenacodontid premaxilla described above. As in *Haptodus* specimens described by Currie (1979), the transverse process bears approximately six teeth. However, in contrast to those specimens described by Currie (1979), the transverse flange is more stoutly built and slightly expanded distally, giving it a nearly triangular outline. A very fine ridge parallels its posterior margin. The ventral margin of the quadrate ramus is thickened, and the medial surface dorsal to it is slightly concave. There is no distinct facet for the basipterygoid process of the braincase. Little can be said about the palatine ramus other than that it was necessarily a narrow element.

A partial right scapula, CM 34444 (Fig. 4H), is characteristic of sphenacodontid and haptodontid pelycosaurs in being anteroposteriorly narrow. The supraglenoid buttress is well-developed and angles back to form the posterior border of the element. The supraglenoid foramen is placed directly on the crest of the buttress, a position also seen in *Haptodus baylei* (Currie, 1979:fig. 9) and considered possibly more primitive than the more anterior position in sphenacodontids.

Of the pelycosaurian material described here, the femur CM 34445 (Fig. 4I) is probably the most poorly preserved, and its taxonomic assignment is made with the least amount of confidence. Despite the extreme dorsoventral crushing, it still exhibits general sphenacodontian features. It is similar in size and general morphology to *Haptodus garnettensis* (Currie, 1977), although the development of

processes and ridges appears to be somewhat greater. The ventral adductor ridge is well-developed and expanded proximally into what Romer and Price (1940) termed the fourth trochanter for attachment of the caudifemoralis musculature (Sumida, 1989a). The midlength of the adductor ridge is marked by an oval pit of unknown function. The extent of the intertrochanteric fossa cannot be determined due to crushing. The intercondylar fossa of the distal, dorsal surface does not extend far up the femoral shaft.

Family Edaphosauridae
Ianthasaurus sp.

Materials.—CM 34449, partial right maxilla (Fig. 5A); CM 34500 and 34576, partial neural spines (Fig. 5B, C); CM 34577, dorsal vertebra with only base of neural spine (Fig. 5D); CM 34578, dorsal portion of right scapular blade (Fig. 5E); CM 34579, left femur (Fig. 5F, G); CM 34580, left astragalus (Fig. 5H, I); CM 34581, partial right femur; CM 47700, numerous, isolated centra and neural spines.

Description.—On the basis of neural spine morphology, two different edaphosaurids are identified from the Badger Creek locality. One form is recognized on the basis of a single unique neural spine (described below), whereas numerous isolated elements, most importantly vertebral neural spines with typical edaphosaurid lateral tubercles, are assigned to *Ianthasaurus.* There are only two well-known Pennsylvanian-aged edaphosaurs: *Edaphosaurus colohistion* from the Pittsburgh Formation, Monongahela Group of West Virginia (Berman, 1979), which probably reached a length of over 2 m, and *Ianthasaurus hardestii* (Reisz and Berman, 1986; Modesto and Reisz, 1990b), the most primitive member of the family from the Garnett Quarry of eastern Kansas, which probably reached a maximum length of 1 m.

With the realization that *Ianthasaurus* is significantly different from *Edaphosaurus,* Modesto and Reisz (1990a) questioned the assignment of other small, Late Pennsylvanian edaphosaurids to *Edaphosaurus* on the basis of fragmentary vertebral evidence. They argued that *E. raymondi* Case (1908), based on a small neural spine fragment, should be considered a nomen vanum and that *E. mirabilis* Fritsch (1895), based on a very small vertebra from Kounova, Czechoslovakia, may be closely related to *I. hardestii.* Further, Modesto and Reisz (1990a) recommended that the edaphosaurid material described here from the Late Pennsylvanian Sangre de Cristo Formation of Colorado and considered by Vaughn (1969) to show close affinities to *E. raymondi* be assigned to the Edaphosauridae as incertae sedis. However, all of the Badger Creek edaphosaurid remains, excluding only the single unique neural spine referred to above (and described below), are comparable in size and morphology to *Ianthasaurus hardestii* and can be assigned reasonably to that genus. The only noticeable difference between them is a higher degree of ossification and development of processes of the appendicular elements in the Badger Creek form.

Though none of the neural spines (Fig. 5B–D) are complete, some are complete enough to allow a composite description. The longest spine fragment is 4.8 cm long. As its diameter remains little changed throughout its length, the neural spine was undoubtedly well over 5 cm long. The spines are subcircular in cross section except for a very short proximal distance, where they are laterally compressed and have a slightly greater anteroposterior dimension. This proximal portion of
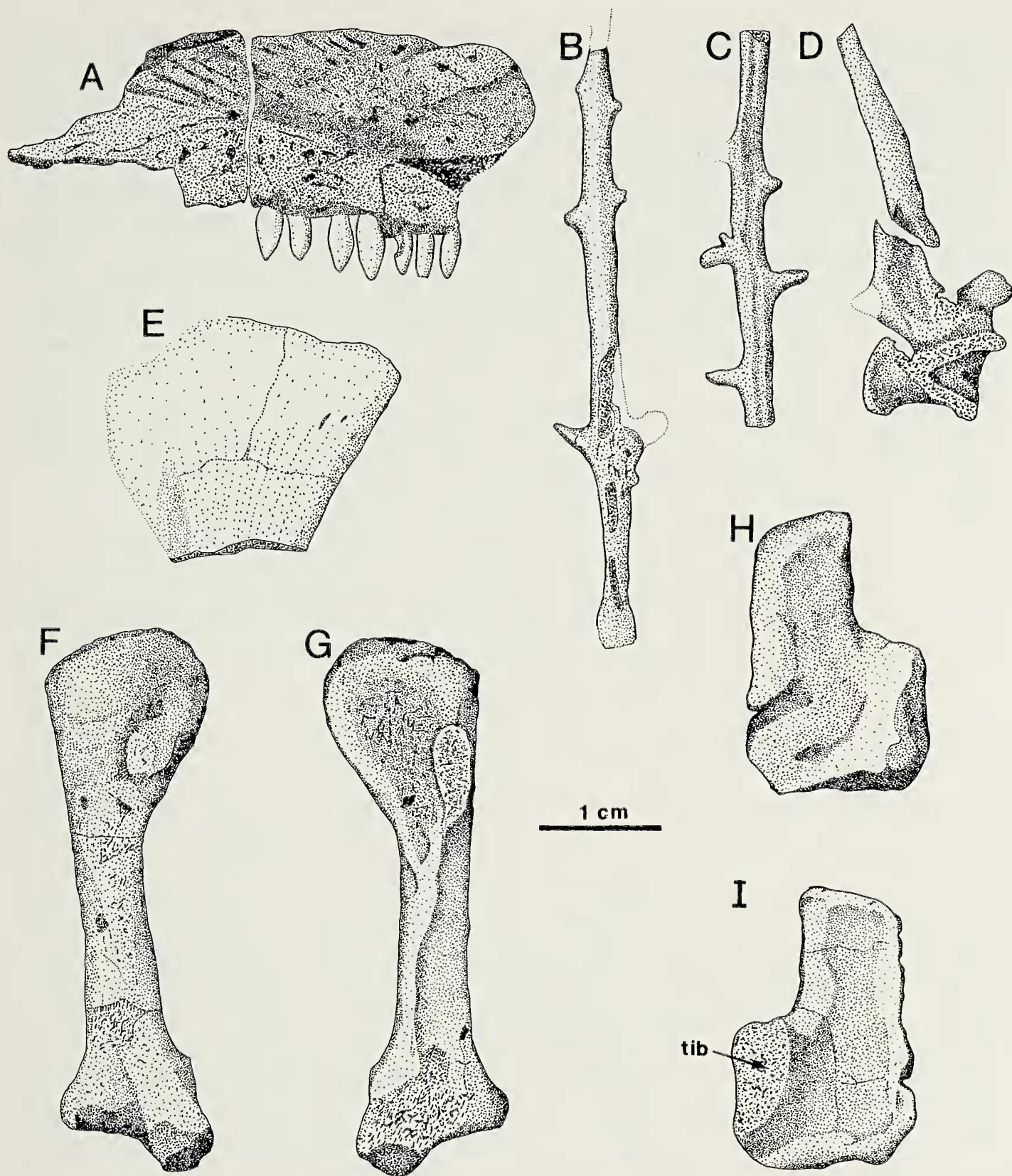
Fig. 5.—*Ianthasaurus* sp. A, lateral view of partial right maxilla CM 34449; B, C, anterior(?) views of isolated neural spines CM 34500 and CM 34576, respectively, that demonstrate variability in morphology of lateral tubercles; D, right lateral view of posterior dorsal vertebra CM 34577; E, lateral view of dorsal portion of right scapula CM 34578; F–G, dorsal and ventral views of left femur CM 34579; H, I, dorsal and ventral views of left astragalus CM 34580. Abbreviation: tib, tibial articulation.

the spine is not as blade-like as in the sphenacodontine vertebra described above. A narrow furrow extends along the anterior and posterior surfaces of the spine.

The presence of lateral tubercles of the neural spines is characteristic of eda-phosaurids, the only exception being the Lower Permian *Lupeosaurus* (Sumida,

1989*b*). They are present on all but a few of the elongate neural spines of the Badger Creek specimens here assigned to *Ianthasaurus*. The absence of the lateral tubercles in some cases, including the bilaterally symmetrical basal pair (Fig. 5D), is a condition identical to that in the posteriormost region of the column in *Ianthasaurus* (Reisz and Berman, 1986). The lateral tubercles of the Badger Creek *Ianthasaurus* are quite knobby in appearance and are occasionally expressed as bifid, branched structures (Fig. 5C). As in other edaphosaurs, the basal tubercles differ from more distal ones in being much more strongly developed and occurring always as bilaterally symmetrical pairs. The neural arches display a slight excavation. This condition differs from that in the sphenacodontine described above in that the excavation continues well up the arch toward the elongate neural spine (Fig. 5D).

The vertebral centra are small, approximately 1 cm in length. They are deeply amphicoelous (Fig. 5D). The centra are spool-shaped, but not visibly keeled. The ventral edges of the anterior and posterior articular surfaces do not demonstrate distinct emarginations for the reception of intercentra.

A dorsal portion of a scapular blade, CM 34578 (Fig. 5E), demonstrates no significant diagnostic features, but is assigned tentatively to *Ianthasaurus,* primarily on the basis of appropriate size. The dorsal border is flared more than in larger species of *Edaphosaurus* (Romer and Price, 1940), a condition somewhat more similar to the rectangular shape in *Ianthasaurus* (Reisz and Berman, 1986).

Left and right femora (CM 34579 and 34581, respectively) of subequal size are assigned to *Ianthasaurus,* but only the nearly complete left one (Fig. 5F, G) forms the basis of the description here. The proximal and distal ends of the right femur are incomplete. The femoral shaft is a slender cylinder with no apparent curvature. The proximodorsal surface has a prominently developed tubercle for attachment of the puboischiofemoralis internus muscle. The relatively large size of the rugosity and its extension toward the posterior margin of the proximal head indicates that it may have also provided attachment for the ischiotrochantericus muscle. Loss of some of the surface bone from the distodorsal surface makes interpretation difficult, but it appears that the intercondylar fossa did not reach far up the shaft. Ventrally, the intertrochanteric fossa is deep and extends well down the body of the femur as in other edaphosaurs (Romer and Price, 1940). A sharp, distinct adductor ridge runs the length of the ventral surface, and its proximal terminus is marked by a broadly expanded internal trochanter for attachment of a portion of the puboischiofemoralis externus muscle (Romer, 1922; Sumida, 1989*a*). The distal popliteal area is a shallow concavity. A conspicuous depression on the posterior face of the posterior femoral condyle designates the proximal fibular articulation.

A complete left astragalus, CM 34580 (Fig. 5H, I), is unusually large compared to the other edaphosaurid elements from Badger Creek. Its extremely elongate proximal process, however, precludes assignment to any other taxon and has been proposed as characteristic of *Edaphosaurus* by Romer and Price (1940). It is L-shaped as in many primitive amniotes (Schaeffer, 1941). The proximal process accounts for 45% of its proximodistal length. The anterior and posterior margins of the proximal process are thickened, the latter more so for articulation with the calcaneum. The proximal surface is expanded similarly for articulation with the fibula. The dorsal surface is dominated by a large, anterodorsally facing, heart-shaped articular surface for the tibia. A conspicuous notch in the posterior edge is for the perforating artery, and a furrow-like continuation of the notch is visible

across the posteroventral surface. Just distal to the furrow is a deep pit of unknown function.

The posterior fragment of a right maxillary, CM 34449 (Fig. 5A), is assigned very tentatively to *Ianthasaurus*. Over half of the dorsal lateral surface is marked by a depressed sutural scar, consisting mainly of parallel ridges and grooves that tend posterodorsally. This marks the area overlapped almost entirely by the lacrimal and possibly in small part by the jugal. Below this the external surface sculpturing consists of irregular pits and ridges. Seven teeth are visible in lateral view, and posterior to them are the bases for the last three of the series. The remaining centimeter of the ventral margin of the maxilla just posterior to the last tooth base is smoothly rounded and did not bear any teeth. The teeth are similar to those in *Edaphosaurus* in being somewhat stout, bulbous, and isodont and in exhibiting no signs of curvature. On the other hand, in *Ianthasaurus* the marginal series consists of numerous, slightly recurved, sharply pointed teeth, with distinct caniniform teeth in the maxillary series (Reisz and Berman, 1986; Modesto and Reisz, 1990*b*). However, evidence of only the last ten teeth are preserved on CM 34449, and without the anterior half of the series, it is impossible to know whether caniniform teeth were present. Yet, the absence of a shelf-like structure on the lingual surface seen in well-preserved marginal teeth of *Edaphosaurus* argues for the tentative assignment of CM 34449 to *Ianthasaurus*.

Family Edaphosauridae
New but unnamed genus and species

Materials.—CM 47699 (formerly UCLA VP 1742), single dorsal neural spine (Fig. 6).

Description.—The edaphosaurid affinities of a neural spine (CM 47699, Fig. 6) are almost undeniably established by the presence of characteristic lateral tubercles, yet other features clearly separate it from other members of the family. The spine is uniformly flattened laterally, maintaining essentially the same transverse width (approximately 1.9–2.0 mm) throughout its length. It expands gradually anteroposteriorly from a narrow base of 4.5 mm to 10.7 mm at its preserved distal end. The distal tip of the spine is chipped, reducing somewhat the actual anteroposterior measurement. The lateral tubercles are hemispherical in shape, with the most proximally placed ones projecting as much as 1.5 mm beyond the lateral surface of the spine. Some of the more distally positioned tubercles are only weakly developed. Unlike many other edaphosaurids, none of the lateral tubercles are arranged in bilaterally symmetrical pairs.

Peabody (1957) erected a new species of *Edaphosaurus, E. ecordi,* from the Late Pennsylvanian Garnett Quarry of eastern Kansas, on the basis of a blade-like neural spine with tubercles. Vaughn (1972) identified the Badger Creek specimen as belonging to this species, noting that the two spines are strikingly similar in both shape and size. Reisz et al. (1982) argued, however, that the lateral tubercles of the holotype of *E. ecordi* are artifacts of preservation and redescribed the spine as representing a new pelycosaurian taxon, *Xyrospondylus*. Reisz and Berman (1986) have since pointed out that the primitive edaphosaur *Ianthasaurus* does not carry lateral tubercles on all of its neural spines. Thus the possibility is raised that CM 47699 could pertain to *Xyrospondylus* and that the presence or absence of tubercles reflects regional differences in the vertebral column. However, the assumption of such a generic association between isolated specimens so geographically separate would not be prudent.
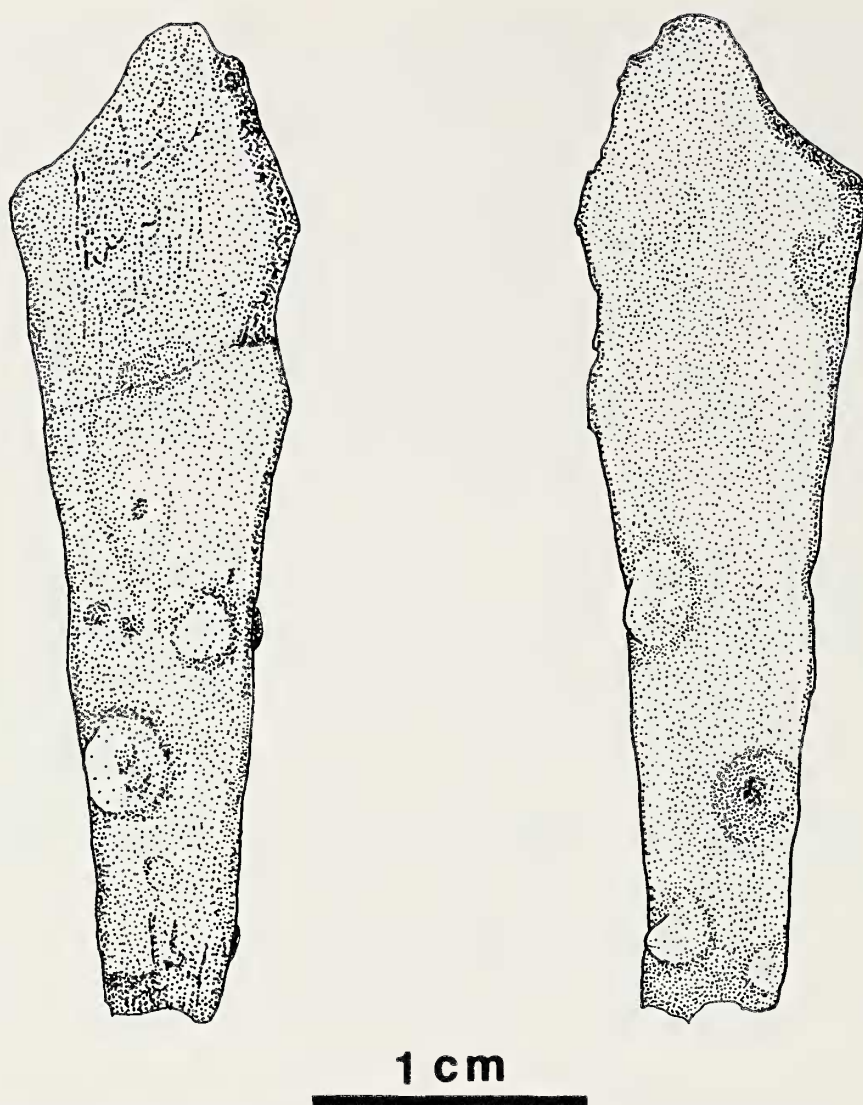
1 cm

Fig. 6.—Lateral views of dorsal neural spine CM 47699 of new, but unnamed genus and species of edaphosaurid.

The entire column in *Ianthasaurus* is known (Reisz and Berman, 1986; Modesto and Reisz, 1990*b*), and nowhere does it exhibit blade-like neural spines. Sumida (1989*b*) assigned the enigmatic genus *Lupeosaurus* to the Edaphosauridae, but the neural spines of its high dorsal sail are essentially circular in cross section and lack lateral tubercles. The large, numerous, Lower Permian *Edaphosaurus* species from Texas demonstrate a tendency toward progressive increase in overall size and anteroposterior expansion of the neural spine tips of the cervical and anteriormost dorsal region to become club-like through time (Romer and Price, 1940). Additionally, there is a concomitant tendency for the spines of this region to exhibit a pronounced anterior curvature. In contrast, the spine CM 47699 increases steadily in anteroposterior dimension distally and is straight throughout its length. On the balance, the spine is unique among known members of the family and, therefore, likely represents a new species. However, because of the very limited material at hand, it would be unwise to erect a new genus and species. More conservatively, the presence of a second type of edaphosaur at Badger Creek is recognized, but erection of a new taxon should await discovery of more complete materials.

DISCUSSION

Although most Pennsylvanian-aged ophiacodonts have been assigned commonly to the genus *Clepsydrops,* it is a poorly defined genus. Despite the presence

of claw-like distal phalanges, the remainder of the limb elements of the Badger Creek ophiacodontid are essentially indistinguishable from *Ophiacodon,* and assignment to that genus could have been made with some confidence. In that regard, it is noteworthy that an as yet undescribed ophiacodont from the Garnett quarry (Reisz, 1990) also possesses claw-like distal phalanges.

More precise classification of the Badger Creek sphenacodontine cannot be justified on the basis of the materials at hand. It is worth noting, however, that this identification, if correct, marks the earliest known occurrence of this otherwise Early Permian group. The presence of a haptodontine at Badger Creek is also significant in adding to the number of rare occurrences of the subfamily in North America. In fact, Lewis and Vaughn (1965) viewed the presence of a haptodontine in the North American Lower Permian Cutler Formation of central Colorado as so unexpected that they designated it as a new genus, *Cutleria.* The Missourian age of the Badger Creek quarry provides the earliest record of the Haptodontinae in North America.

Edaphosaurs are among the most common pelycosaurs in Pennsylvanian-age faunas. Edaphosaurs have been documented from the Conemaugh and Monongahela groups of the tri state area of eastern North America (Case, 1908; Berman, 1979), as well as from a variety of locations in eastern Kansas (Reisz and Berman, 1986; Schultze and Chorn, 1988; Chorn and Schultze, 1990; Modesto and Reisz, 1990*b*). With one exception (Berman, 1979), Pennsylvanian records of edaphosaurs have been invariably of very small animals only a meter or so long and considerably smaller than the later forms of the Lower Permian. This is true of the more common Badger Creek form that possesses spines with typical subcircular cross section. It is potentially distinguishable from *Ianthasaurus* from the Garnett locality only on the basis of the more complete ossification of appendicular elements. In terms of absolute numbers, *Ianthasaurus* accounts for the majority of pelycosaurian materials at Badger Creek.

All of the Badger Creek pelycosaur specimens consist of isolated and often incompletely preserved bones. Thus, it is not surprising that this locality yields numerous specimens that are very probably pelycosaurian, but for which more precise taxonomic identifications are unsafe or impossible. Nevertheless, these elements are worth noting, as they further testify to the large pelycosaurian component of the quarry. All the bones are catalogued under a single number, CM 34582, despite the fact that they undoubtedly represent several taxa. Most notable are the fragmentary remains of vertebrae, scapulae, a clavicle, and humeri. Also present are tarsal elements and sharply pointed, claw-like distal phalanges.

Romer and Price (1940) and Reisz (1972, 1980, 1986) have argued that pelycosaurian-grade synapsids have diversified considerably by the Late Pennsylvanian. The presence of five distinct pelycosaurs at the Badger Creek locality provides evidence to support this contention. With the exception of the potentially new edaphosaurid taxon, the materials on which each of the taxonomic identifications were made are in general quite similar to other Late Pennsylvanian and Early Permian representatives of their respective taxa. As Reisz (1980) pointed out, the general features of most pelycosaurian families were established well before the time of the more commonly preserved Permian pelycosaurs.

The presence of five different pelycosaurs at Badger Creek ranks it among the most diverse assemblages of Pennsylvanian-aged pelycosaur localities in the world (see Table 1). Among North American localities it is surpassed in numbers of pelycosaurs only by El Cobre Canyon in northern New Mexico. Although the

exact age of the exposures from which pelycosaurs have been recovered in El Cobre Canyon is uncertain, Berman et al. (1987) have demonstrated that they are clearly Upper Pennsylvanian. An equal number of pelycosaurs has been reported from the somewhat younger Pennsylvanian locality of Garnett, Kansas (Reisz, 1990). Though the preservation of the material from Garnett is considerably better than that from Badger Creek, the latter deposit nonetheless adds to our knowledge of the distribution of early pelycosaurs. Late Pennsylvanian localities producing significant remains of tetrapods tend to be clustered about the equatorial plane of that time (Milner and Panchen, 1973; Lombard and Sumida, 1992). In this regard, Badger Creek is among the westernmost localities of undoubted Pennsylvanian age to produce pelycosaurs in North America.

ACKNOWLEDGMENTS

LITERATURE CITED

BERMAN, D. S. 1979. *Edaphosaurus* (Reptilia, Pelycosauria) from the Lower Permian of northeastern United States, with description of a new species. Annals of Carnegie Museum, 48:185–202.

———. In press. Lower Permian vertebrates of New Mexico. Field Trip Guidebook, 53rd Annual Meeting of the Society of Vertebrate Paleontology, Albuquerque, New Mexico.

BERMAN, D. S, AND S. S. SUMIDA. 1990. A new species of *Limnoscelis* (Amphibia, Diadectomorpha) from the Late Pennsylvanian Sangre de Cristo Formation of central Colorado. Annals of Carnegie Museum, 59:303–341.

BERMAN, D. S, R. R. REISZ, AND D. A. EBERTH. 1987. A new genus and species of trematopid amphibian from the Late Pennsylvanian of north-central New Mexico. Journal of Vertebrate Paleontology, 7:252–269.

BERMAN, D. S, S. S. SUMIDA, AND R. E. LOMBARD. 1992. Reinterpretation of the temporal and occipital regions in *Diadectes* and the relationships of diadectomorphs. Journal of Paleontology, 66:481–499.

BRILL, K. G. 1952. Stratigraphy of the Permo-Pennsylvanian zeugogeosyncline of Colorado and northern New Mexico. Geological Society of America Bulletin, 63:809–880.

BRINKMAN, D., AND D. A. EBERTH. 1983. The interrelationships of pelycosaurs. Breviora, 473:1–35.

CARROLL, R. L. 1964. The earliest reptiles. Zoological Journal of the Linnean Society, 45:61–83.

CASE, E. C. 1908. Description of vertebrate fossils from the vicinity of Pittsburgh, Pennsylvania. Annals of Carnegie Museum, 4:234–241.

CHORN, J., AND H.-P. SCHULTZE. 1990. The Robinson locality: fauna and depositional environment. Pp. 17–23, *in* 1990 Society of Vertebrate Paleontology Upper Paleozoic of Eastern Kansas Excursion Guidebook (C. R. Cunningham and C. G. Maples, eds.), Kansas Geological Survey Openfile Report 90-24, Lawrence, 48 pp.

COPE, E. D. 1875. On fossil remains of Reptilia and fishes from Illinois. Proceedings of the Academy of Natural Sciences of Philadelphia, 1875:404–411.

CURRIE, P. J. 1977. A new haptodontine sphenacodont (Reptilia: Pelycosauria) from the Upper Pennsylvanian of North America. Journal of Paleontology, 51:927–942.

———. 1979. The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). Palaeontographica, 163:130–168.

DeMAR, R. 1970. A primitive pelycosaur from the Pennsylvanian of Illinois. Journal of Paleontology, 44:154–163.

EBERTH, D. A. 1985. The Skull of *Sphenacodon ferocior*, and Comparisons with Other Sphenaco-dontines. New Mexico Bureau of Mines and Mineral Resources, Circular 190, 39 pp.

FRITSCH, A. 1895. Ueber neue Wirbelthiere aus der Permformation Bohmens, nebst einer Uebersicht der aus derselben bekannt gewordenen Arten. Sitzungsberichte der Bohmischen Gesellschaft der Wissenschaften, 53:1–17.

GAUTHIER, J. A., A. G. KLUGE, AND T. ROWE. 1988. The early evolution of the Amniota. Pp. 102–155, *in* The Phylogeny and Classification of the Tetrapods, Volume 1, Amphibians, Reptiles, Birds (M. J. Benton, ed.), Systematics Association Special Volume 35A, Clarendon Press, Oxford, 377 pp.

HOOK, R. W., AND D. BAIRD. 1986. The diamond coal mine of Linton, Ohio, and its Pennsylvanian-age vertebrates. Journal of Vertebrate Paleontology, 6:174–190.

LAURIN, M. In press. Cranial anatomy and relationships of *Haptodus garnettensis* (Amniota: Synapsida). Journal of Vertebrate Paleontology.

LEWIS, G. E., AND P. P. VAUGHN. 1965. Early Permian Vertebrates from the Placerville Area, Colorado. Contributions to Paleontology, Geological Society Professional Paper 503-C, 46 pp.

LOMBARD, R. E., AND S. S. SUMIDA. 1992. Recent progress in understanding early tetrapods. American Zoologist, 32:609–622.

MALLORY, W. W. 1958. Pennsylvanian coarse arkosic redbeds and associated mountains in Colorado. Pp. 17–20, *in* Rocky Mountain Association of Geologists, Symposium on Pennsylvanian Rocks of Colorado and Adjacent Areas.

————. 1960. Outline of Pennsylvanian stratigraphy of Colorado. Pp. 23–33, *in* Geological Society of America and Rocky Mountain Association of Geologists, "Guide to the Geology of Colorado."

MILNER, A. R., AND A. L. PANCHEN. 1973. Geographical variation in the tetrapod faunas of the Upper Carboniferous and Lower Permian. Pp. 353–368, *in* Implications of Continental Drift to the Earth Sciences, Volume 1 (D. H. Tarling and S. K. Runcorn, eds.), Academic Press, London.

MODESTO, S. P., AND R. R. REISZ. 1990a. Taxonomic status of *Edaphosaurus raymondi* Case. Journal of Paleontology, 64:1049–1051.

————. 1990b. A new skeleton of *Ianthasaurus hardestii*, a primitive edaphosaur from the Upper Pennsylvanian of Kansas. Canadian Journal of Earth Sciences, 27:834–844.

PEABODY, F. E. 1957. Pennsylvanian reptiles of Garnett, Kansas: Edaphosaurs. Journal of Paleontology, 31:947–949.

REISZ, R. R. 1972. Pelycosaurian reptiles from the Middle Pennsylvanian of North America. Bulletin of the Museum of Comparative Zoology, 144:27–62.

————. 1980. The Pelycosauria: A review of phylogenetic relationships. Pp. 553–592, *in* The Terrestrial Environment and the Origin of Land Vertebrates (A. L. Panchen, ed.), Systematics Association Special Volume Number 15, Academic Press, New York, 634 pp.

————. 1986. Pelycosauria. Handbuch der Paläoherpetologie, 17A:1–102.

————. 1990. Geology and paleontology of the Garnett quarry. Pp. 43–48, *in* 1990 Society of Vertebrate Paleontology Upper Paleozoic of Eastern Kansas Excursion Guidebook (C. R. Cunningham and C. G. Maples, eds.), Kansas Geological Survey Open-file Report 90-24, Lawrence, 48 pp.

REISZ, R. R., AND D. S BERMAN. 1986. *Ianthasaurus hardestii* n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas. Canadian Journal of Earth Sciences, 23:77–91.

REISZ, R. R., D. S BERMAN, AND D. SCOTT. 1992. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the early Permian of Texas. Zoological Journal of the Linnean Society, 104:127–184.

REISZ, R. R., M. J. HEATON, AND B. R. PYNN. 1982. Vertebrate fauna of Late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. Journal of Paleontology, 56:741–750.

ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. Bulletin of the American Museum of Natural History, 46:517–606.

————. 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh–West Virginia region. Annals of Carnegie Museum, 33:52–112.

————. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, 772 pp.

————. 1961. A large ophiacodont pelycosaur from the Pennsylvanian of the Pittsburgh region. Breviora, 144:1–7.

ROMER, A. S., AND L. I. PRICE. 1940. Review of the Pelycosauria. Geological Society of America Special Paper, Number 28, 538 pp.

SCHAEFFER, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. Bulletin of the American Museum of Natural History, 78:395–472.

SCHULTZE, H.-P., AND J. CHORN. 1988. The Upper Pennsylvanian vertebrate fauna of Hamilton, Kansas. Pp. 147–154, *in* Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas (G. Mapes and R. Mapes, eds.), Kansas Geological Survey Guidebook Series 6, 273 pp.

SUMIDA, S. S. 1989*a*. The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. Journal of Vertebrate Paleontology, 9:295–313.

———. 1989*b*. New information on the pectoral girdle and vertebral column in *Lupeosaurus* (Reptilia, Pelycosauria). Canadian Journal of Earth Sciences, 26:1343–1349.

VAUGHN, P. P. 1969. Upper Pennsylvanian vertebrates from the Sangre de Cristo Formation of central Colorado. Contributions in Science, Los Angeles County Museum of Natural History, 164:1–28.

———. 1972. More vertebrates, including a new microsaur, from the Upper Pennsylvanian of central Colorado. Contributions in Science, Los Angeles County Museum of Natural History, 223:1–30.

WILLISTON, S. W., AND E. C. CASE. 1913. Description of a nearly complete skeleton of *Ophiacodon* Marsh. Carnegie Institute of Washington Publication, 181:37–59.